

Chapter 11

The Importance of Fish, Fowl and Small Mammals in the Paleolithic Diet of the Swabian Jura, Southwestern Germany

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Introduction

The development and spread of modern humans and the extinction of archaic humans represents one of the most important processes in the history of our genus. The Swabian Jura of southwestern Germany preserves a rich and unique record of the behavioral patterns of Neanderthals and early modern humans. Since the 1860s archaeologists and Quaternary scientists have studied the caves of the Swabian Jura to gain information on region's archaeology and hominin adaptations during the Late Pleistocene (Müller-Beck 1983; Scheer 1994; Conard and Bolus 2006).

One of the many important aspects of the archaeology of the Swabian caves is the abundance of well-preserved faunal assemblages (Weinstock 1999; Münzel and Conard 2004a, b; Niven 2006; Krönneck 2012). Most of the key assemblages come from the caves of the Ach and Lone valleys, but lesser known areas such as the Lauchert Valley also contain caves with rich faunal material (Fig. 11.1). Unfortunately, open-air localities with stratified faunal material are rare in the Swabian Jura. These faunal assemblages from the many caves, however, provide an ideal starting point for reconstructing past subsistence practices. Here we consider new information from the caves of the Swabian Jura that provides insights into the changing subsistence practices of the Paleolithic hunters and gatherers of the region.

Until now, nearly all of the faunal studies from the Swabian caves have addressed issues related to the large mammalian fauna (Lehmann 1954; Gamble 1979; Münzel et al. 1994; Weinstock 1999; Münzel and Conard 2004a, b; Niven 2006; Krönneck 2012; Münzel *in press*). These studies went a long way toward reconstructing how the region's Middle and Upper Paleolithic peoples made a living and fed themselves. Although different sites and different strata showed a degree of variation in the abundances of game taxa, the mammalian archaeofauna was mainly characterized by continuity (Münzel and Conard 2004a), and most work up to now has stressed the broad similarities between diet during the Middle and Upper Paleolithic. While the specific geographic setting of sites can affect the availability of game species and helps, for example, to explain the relative abundance of ibex (*Capra ibex*) at Große Grotte and Geißenklösterle near the high cliffs of the Ach Valley, most assemblages from both periods are dominated by horse (*Equus* sp.) and reindeer (*Rangifer tarandus*) (Tables 11.1, 11.2; Figs. 11.2, 11.3) (Krönneck et al. 2004; Münzel and Conard 2004a).

The faunal remains of cave bear (*Ursus spelaeus*) and mammoth (*Mammuthus primigenius*) are often very numerous and require special attention since they can

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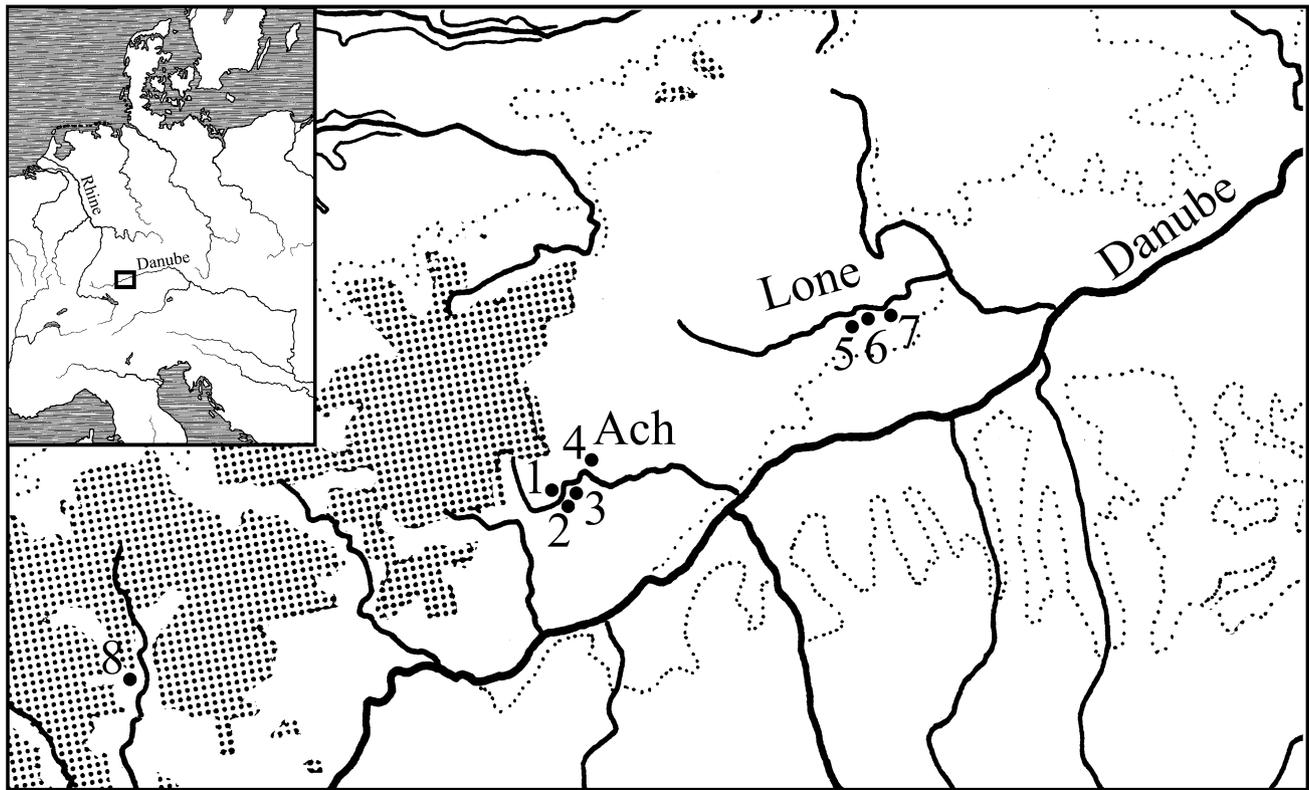


Fig. 11.1 Map of southwestern Germany with the principal sites mentioned in the text. Ach Valley: (1) Sirgenstein, (2) Hohle Fels, (3) Geißenklösterle, (4) Brillenhöhle; Lone Valley: (5) Bockstein, (6) Hohlenstein-Stadel and Hohlenstein-Bärenhöhle, (7) Vogelherd; Lauchert Valley: (8) Göpfelsteinhöhle

Table 11.1 Geißenklösterle and Hohle Fels

Taxa	Geißenklösterle			Hohle Fels			
	Middle Paleolithic	Aurignacian	Gravettian	Middle Paleolithic	Aurignacian	Gravettian/Aurignacian	Gravettian
<i>Mammuthus primigenius</i>	3	220	51	0	21	2	40
<i>Coelodonta antiquitatis</i>	8	62	4	2	4	0	1
<i>Equus</i> sp.	21	483	115	10	126	34	336
<i>Cervidae</i>	64	508	186	9	237	65	315
Small ruminants	89	385	155	7	81	25	106
<i>Ursus spelaeus</i> and <i>U. arctos</i>	586	2,972	1,419	534	1,021	946	2,273
<i>Canis lupus</i> and other carnivores	39	160	30	7	44	11	54
<i>V. vulpes</i> and <i>A. lagopus</i>	26	159	109	4	34	14	73
<i>Lepus</i> sp.	8	209	240	1	52	25	474
Total	844	5,158	2,309	574	1,620	1,122	3,672

NISP of mammalian fauna by taxa without ivory. The main species in *Cervidae* are reindeer and red deer, with reindeer always dominant. The main species for small ruminants are ibex and chamois, with ibex typically being better represented

swamp the faunal signals with material that is not related to past human diets (Tables 11.1, 11.2; Figs. 11.2, 11.3). Throughout the Middle Paleolithic, Aurignacian and Gravettian, remains of cave bear are abundant at

Geißenklösterle and Hohle Fels. A high proportion of the cave bear remains accumulated through natural mortality and has no importance for reconstructing human diet. This being said, both during the Middle and Upper Paleolithic, cave bears

Table 11.2 Geißenklösterle and Hohle Fels

Taxa	Geißenklösterle			Hohle Fels			
	Middle Paleolithic	Aurignacian	Gravettian	Middle Paleolithic	Aurignacian	Gravettian/Aurignacian	Gravettian
<i>Mammuthus primigenius</i>	25	7,261	1,725	0	1,457	41	2,300
<i>Coelodonta antiquitatis</i>	129	869	21	11	71	0	21
<i>Equus</i> sp.	317	6,452	1,113	264	1,920	586	4,673
<i>Cervidae</i>	1,432	3,134	1,386	84	2,123	574	2,100
Small ruminants	530	1161	494	34	617	347	894
<i>Ursus spelaeus</i> and <i>U. arctos</i>	2,945	12,687	4,443	4,804	10,622	11,840	25,940
<i>Canis lupus</i> and other carnivores	162	492	50	48	252	792	169
<i>V. vulpes</i> and <i>A. lagopus</i>	35	119	87	7	55	23	106
<i>Lepus</i> sp.	9	222	239	0	44	40	655
Total	5,583	32,396	9,558	5,253	17,161	14,243	36,858

Bone weight (g) of mammalian fauna by taxa without ivory. The main species in *Cervidae* are reindeer and red deer, with reindeer always dominant. The main species for small ruminants are ibex and chamois, with ibex typically being better represented

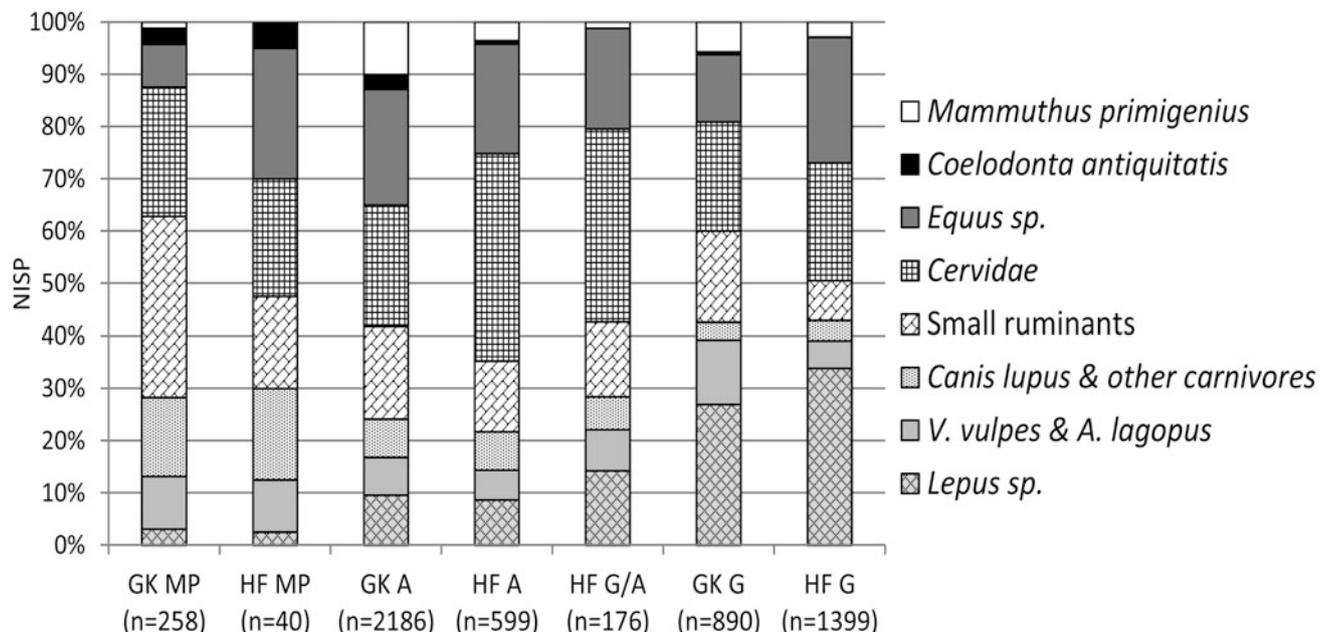


Fig. 11.2 Geißenklösterle and Hohle Fels. NISP% of mammalian fauna by taxa excluding cave bear and mammoth ivory to facilitate comparisons. The main species in *Cervidae* are reindeer and red deer, with reindeer always dominant. The main species for small ruminants

were occasionally hunted and butchered (Münzel and Conard 2004b). Mammoth is abundant at some sites and particularly frequent during the Aurignacian and to a lesser extent during the Gravettian. This pattern has usually been attributed to the frequent use of mammoth bone and ivory as raw material, rather than a high abundance of mammoth in the diet (Münzel 2001, 2005). Yet, like in other regions (Cavarretta et al. 2001), considerable uncertainty surrounds the question of whether or

are ibex and chamois, with ibex typically being better represented. (GK Geißenklösterle, HF Hohle Fels, MP Middle Paleolithic, A Aurignacian, G/A Gravettian/Aurignacian, G Gravettian)

not early Upper Paleolithic peoples of the Swabian Jura hunted significantly more mammoth than the hominins of the Middle Paleolithic (Niven 2006).

Other trends suggest that woolly rhinoceros (*Coelodonta antiquitatis*) may have been exploited more consistently during the Middle Paleolithic than the Upper Paleolithic. One could also point to other aspects of variability in the large mammalian fauna and their inferred contributions to

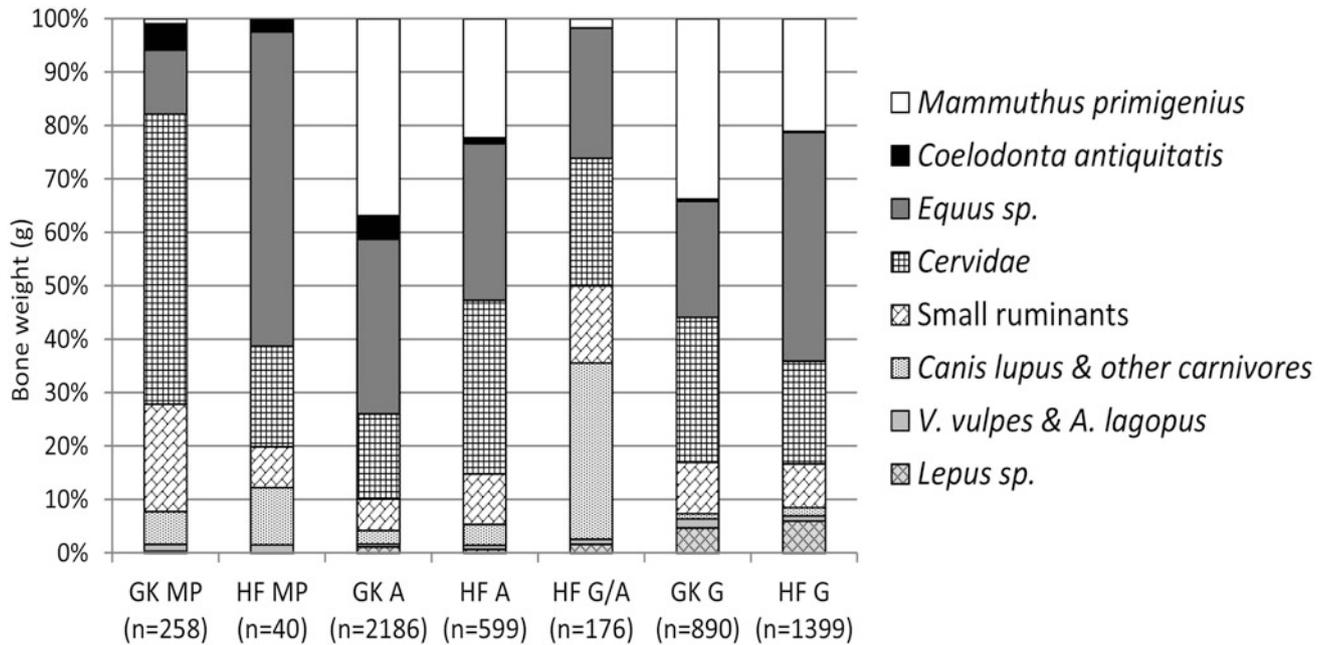


Fig. 11.3 Geißenklösterle and Hohle Fels. Bone weight % of mammalian fauna by taxa excluding cave bear and mammoth ivory to facilitate comparisons. The main species in *Cervidae* are reindeer and red deer, with reindeer always dominant. The main species for

small ruminants are ibex and chamois, with ibex typically being better represented. (GK Geißenklösterle, HF Hohle Fels, MP Middle Paleolithic, A Aurignacian, G/A Gravettian/Aurignacian, G Gravettian)

Pleistocene hominin diets. Still, Neanderthals and modern humans both seem to have actively hunted similar mammalian species in broadly similar patterns (Münzel and Conard 2004a; Conard et al. 2006). Since environments were broadly comparable in both periods, this conclusion comes as no surprise (Miller 2009; Krönneck 2012). In this context, our faunal data suggest that the environmental shifts of the Middle and Upper Paleolithic were generally not extreme enough to cause sudden faunal turnovers. This circumstance allowed the persistence of relatively consistent faunal community through the Middle and the early Upper Paleolithic. Only with the end of the local Gravettian around 26 ka BP and the onset of the Last Glacial Maximum (LGM) do we observe a very clear decline in vegetation and the mammalian faunal community. As one would expect, in the absence of rich botanical and faunal communities, human occupation of the region declined radically until the beginning of the Swabian Magdalenian around 13.5–12.5 ¹⁴C kBP (Weniger 1987; Hahn 1995; Terberger 2001).

Palynological investigations in southern Germany showed that the vegetation in the last glacial cycle was characterized by steppe-like botanical communities (Müller 2001). During MIS 5d-a, the proportion of trees was higher than later, but there were never dense forests compared to interglacial periods. The arboreal species decreased in MIS 4 and vanished at the end of MIS 3, just before the LGM (MIS 2). From the Middle Paleolithic to the Aurignacian, hominins lived in steppic conditions with thin woods and

localized riverine forests. In the Gravettian, only plants that reflect steppe-like environment persist in the pollen profiles (Lang 1994; Müller 2001). The same trend is observed with avian fauna, in which the species diversity decreases over time, and the species living in wooded areas disappear with the climatic decline of the LGM (Krönneck 2009, 2012).

In recent years, advances in zooarchaeological research have led to a heightened interest in examining circumstances under which different classes of animal resources became incorporated in past human diets. For example, in their diachronic studies Stiner, Munro, Haws, Hockett and others pursued possible explanations for dietary shifts between the Middle and Upper Paleolithic (Stiner et al. 1999; Stiner and Munro 2002; Hockett and Haws 2003). Additionally, Klein, Steele and colleagues have argued that the intensity of the exploitation of small game and molluscan resources can be used as a proxy for resource stress and changing population densities (Klein and Cruz-Urbe 2000; Steele and Klein 2005/2006).

In this broad context, Hockett and Haws (2003, 2005) speculated that researchers would find more evidence for the use of small game including small mammals, fish, and birds in the Swabian Aurignacian in comparison to the Middle Paleolithic. This hypothesis implies that modern humans were able to outcompete Neanderthals as a result of incorporating and exploiting nutritional resources that Neanderthals did not use. The expansion of diet breadth, all else being equal, would then allow modern humans to

maintain larger populations within the occupied areas and outcompete Neanderthals, who were perhaps culturally conservative and highly focused upon exploiting large mammalian game (Conard et al. 2006; Conard 2011). Until now, little data were available to test these ideas based on abundances of small mammals, birds and fish from the caves of the Swabian Jura.

This paper reports the results of the first systematic attempt to present diachronic and numerical data on the abundance of small mammals, birds and fish in the diets of the Paleolithic inhabitants of the Ach Valley in the Swabian Jura. While the analyses are still ongoing, the current data from the Middle Paleolithic and early Upper Paleolithic reflects continuity in most areas accompanied by increases in the use of small mammals, birds and fish.

Cultural Stratigraphy

The Paleolithic cultural stratigraphy and chronostratigraphy of the Swabian caves have been well studied and document reliable records of behavioral evolution. Hohle Fels and Geißenklösterle, the key sites examined in this paper, have been excavated with great care over decades and contain long sequences of Middle and Upper Paleolithic deposits that serve as ideal case studies for examining past patterns of subsistence.

In general, the Middle Paleolithic deposits belong to the Late Pleistocene, but very few of the find horizons have been dated by reliable means. The radiocarbon dates for the Middle Paleolithic often represent minimum ages, and the absolute date for the late phase of the Middle Paleolithic from Geißenklösterle based on ESR dating on tooth enamel falls around 43 ka BP (Richter et al. 2000).

Following what appears to be an occupational hiatus at the end of the Middle Paleolithic (Conard and Bolus 2006; Conard et al. 2006), the Upper Paleolithic begins with the Aurignacian. The Aurignacian appears abruptly in a developed form with no convincing indications for cultural continuity between the Middle and the early Upper Paleolithic. Only in exceptional circumstances, such as at Haldenstein Cave, are leaf points or *Blattspitzen* assemblages found in stratified contexts (Riek 1938). Thermoluminescence dates on heated flint artifacts place the beginning of the Aurignacian around 41 ka BP (Richter et al. 2000), which is consistent with the calibrated ages of the radiocarbon measurements from the early Aurignacian of the region (Conard and Bolus 2003, 2008).

The caves of the Swabian Jura contain rich Aurignacian deposits, which using radiocarbon dating typically date between 40 and 30 ¹⁴C kBP. These Aurignacian deposits are usually much richer in artifact finds than the preceding Middle Paleolithic horizons. The period of 30–27 ¹⁴C kBP

documents the development of the Swabian Gravettian (Moreau 2009). Like the Aurignacian, the dates for the early Gravettian are old in comparison with most regions and points to the central and upper Danube region as a key area of cultural innovation during the early part of the Upper Paleolithic (Conard and Bolus 2003). Many find horizons also point to intense periods of occupation during the Gravettian, particularly in the Ach Valley (Scheer 2000; Conard and Moreau 2004; Moreau 2009). Together with the unfavorable climatic condition of the LGM, the local Gravettian populations declined and eventually left the region. The next significant phase of occupation in the Swabian Jura is the Magdalenian, which appears around 13.5–12.5 ¹⁴C kBP and lasts for about a millennium before the Late Paleolithic of the terminal Pleistocene begins. The Middle Paleolithic, Aurignacian and Gravettian form the cultural stratigraphic units of the current study.

Taphonomic Biases

In order to examine how subsistence practices developed during the Middle and Upper Paleolithic, one must consider the extent to which differential preservation of faunal remains or other taphonomic biases affect the archaeological record. The faunal assemblages of the Swabian caves are well preserved, justifying a meaningful comparison of the assemblages over time. The preservation is generally good in terms of morphology, surface preservation and biomolecules. Numerous extractions of collagen for radiocarbon dating and stable isotope studies have shown consistently high yields, and publications on ancient DNA from these cave fauna document excellent preservation (Hofreiter et al. 2002, 2007; Bocherens 2011; Münzel et al. 2011).

The only notable exceptions to this pattern are bones from a number of Middle Paleolithic layers, for example, at Geißenklösterle that show signs of mechanical and chemical surface weathering. These weathered bones are still well preserved in terms of their biomolecular signatures, but they are poorly suited for studying surface modifications. If we quantify anthropogenic versus natural modifications, including carnivore damage, we observe a decrease in carnivore activities and mechanical and chemical weathering from the Middle Paleolithic towards the Upper Paleolithic layers, while the amount of anthropogenic modifications clearly increases (Fig. 11.4). In the current context, we are particularly concerned with the possibility that bones of small mammals, birds and fish may be less well preserved in the deposits of the Middle Paleolithic versus the Upper Paleolithic (Münzel 2009). One argument to suggest the contrary is the presence of microfauna in the deposits from both periods.

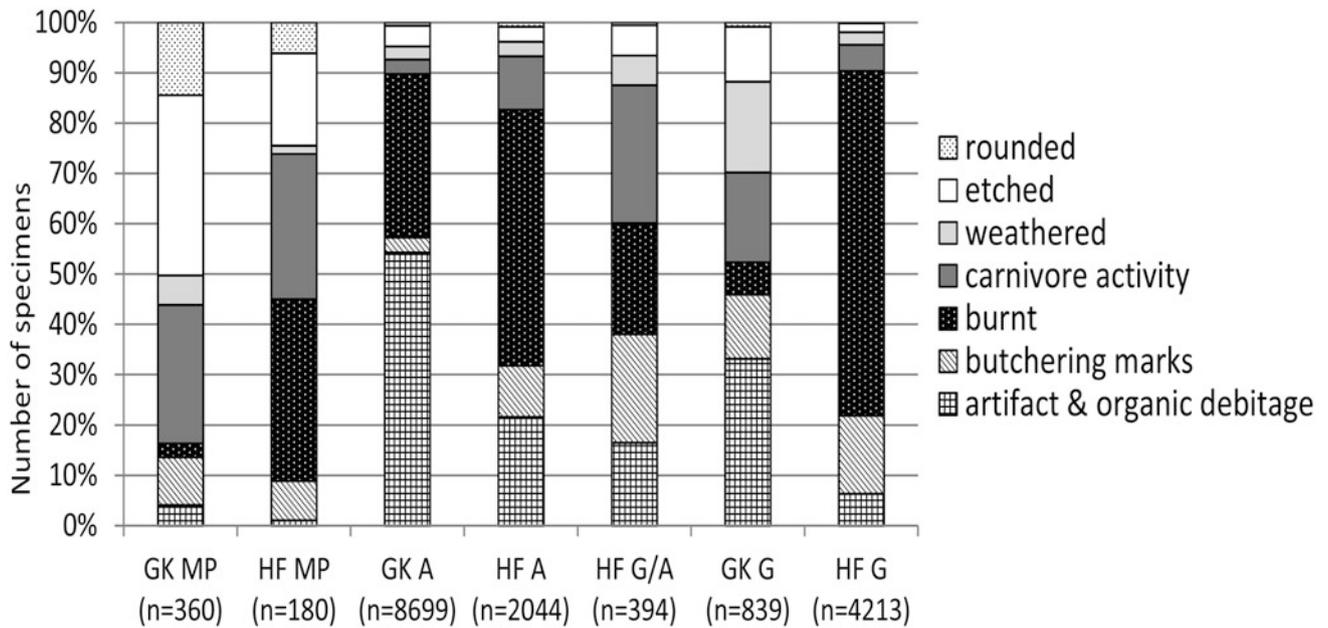


Fig. 11.4 Geißenklösterle and Hohle Fels. Frequency of natural and anthropogenic modifications of bones. To avoid double counting of bones, in the relatively few cases in which bones have multiple modifications, the anthropogenic modification takes precedent over

the natural one. Unlike the other diagrams, this includes mammoth ivory. (*GK* Geißenklösterle, *HF* Hohle Fels, *MP* Middle Paleolithic, *A* Aurignacian, *G/A* Gravettian/Aurignacian, *G* Gravettian)

Since the Middle and Upper Paleolithic deposits both contain microfauna, we assume for now that there is no fundamental bias affecting the preservation of bones of small mammals, birds and fish. The question of possible biases in preservation needs to be considered in greater detail as we collect more data on the taphonomy of bones under study.

Another issue is determining the contribution of non-human agents to the accumulation of the faunal assemblages. We see no indications that cave bears brought bones of fish, birds or small mammals into the caves. Work by Bocherens and colleagues (Bocherens et al. 1994, 2006; Münzel et al. 2011) using stable isotopes indicates that the cave bears were herbivores. These conclusions are consistent with studies on tooth morphology, which suggest that cave bears were not habitual carnivores (Kurtén 1976). Another key point is that the small bones and fish scales show no signs of surface weathering and etching that are associated with the digestion of bones by carnivores and birds of prey (Krönneck *in press*). Gnawed bones exist in both the Middle and Upper Paleolithic horizons, with higher numbers of carnivore damage in the Middle Paleolithic deposits. Another argument against a strong taphonomic bias is the presence of anthropogenically modified bones of small mammals and birds in both the Middle and Upper Paleolithic (Böttcher et al. 2000; Krönneck 2009; Münzel 2009). At this stage of analysis, we have yet to identify taphonomic features of the sites in question that would significantly bias the preservation of small bones in

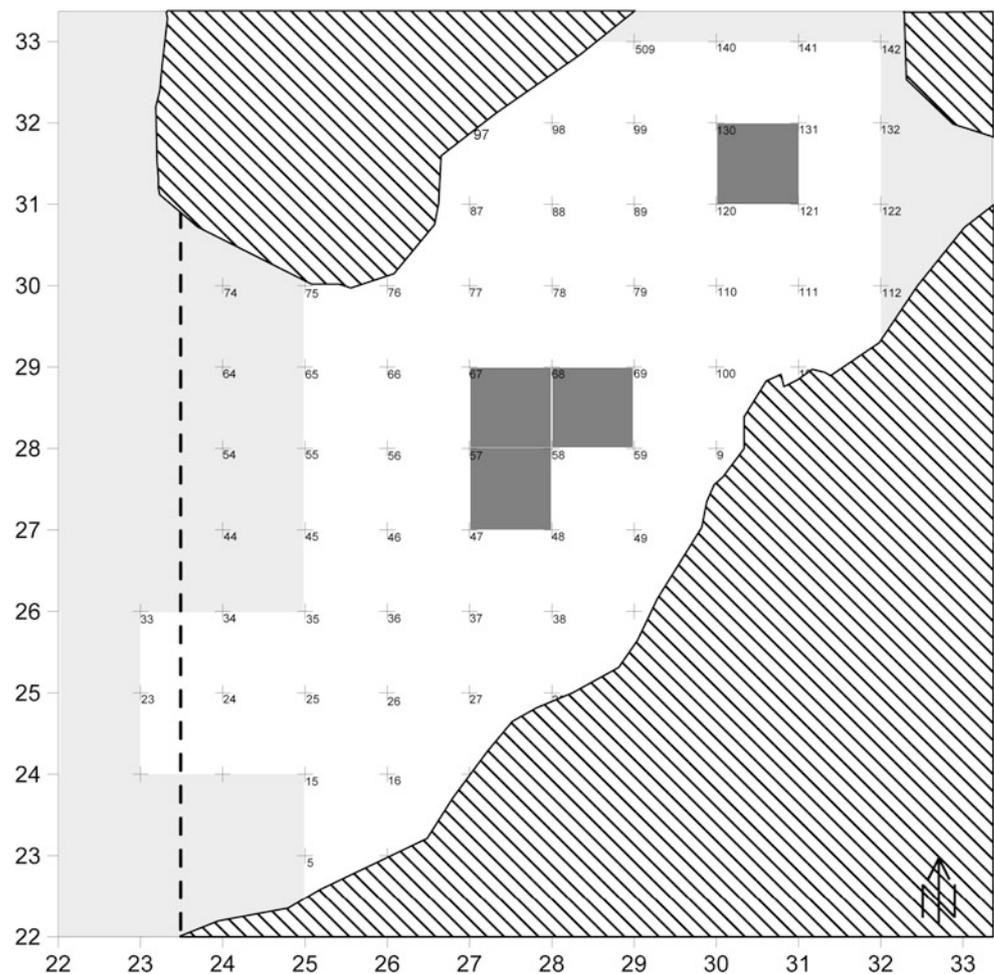
archaeological strata under study. Given the absence of obvious taphonomic bias, we assume that the assemblages of small fauna examined here are broadly comparable.

Sampling

Geißenklösterle and Hohle Fels have been excavated over many seasons using careful methods and systematic water-screening of all the deposits, making them suitable for analyzing small animal exploitation. Fieldwork at Geißenklösterle ran from 1973 to 1991 with a few interruptions. The dig was initially led by Eberhard Wagner and continued starting in 1974 under Joachim Hahn's (1988) direction. Between 2000 and 2002 archaeologists from the University of Tübingen conducted the most recent phase of excavation (Conard and Malina 2003). The modern phase of excavations at Hohle Fels began in 1977 under Hahn's lead and has continued nearly every year since, with the last 15 seasons of the ongoing excavations under Conard's direction.

All archaeological sediments from these excavations have been water-screened with mesh down to 2 mm to recover remains of birds, fish, small mammals and other classes of small materials and artifacts. For each quarter meter of the excavations, we have continuous sequences of uninterrupted finely water-screened and sorted samples. We have processed ca. 12,000 buckets from Geißenklösterle

Fig. 11.5 Geißenklösterle. Map of the excavation showing the location of the four square meters sampled for small faunal remains. Figure by M. Malina



and ca. 17,000 buckets from Hohle Fels. Since this work, while productive for a wide range of reasons, is extremely time consuming, we have defined a number of archaeological units for our samples. At Geißenklösterle, the main sample for bird and fish bones originates from 960 washed and sorted buckets of sediment ranging between 1 and 10 l, while most of the small mammalian faunal remains come from the piece-plotted finds. At Hohle Fels, 1,005 water-screened samples provided the majority of the avian and fish material, and the great majority of the small mammalian faunal remains originate from the piece-plotted finds.

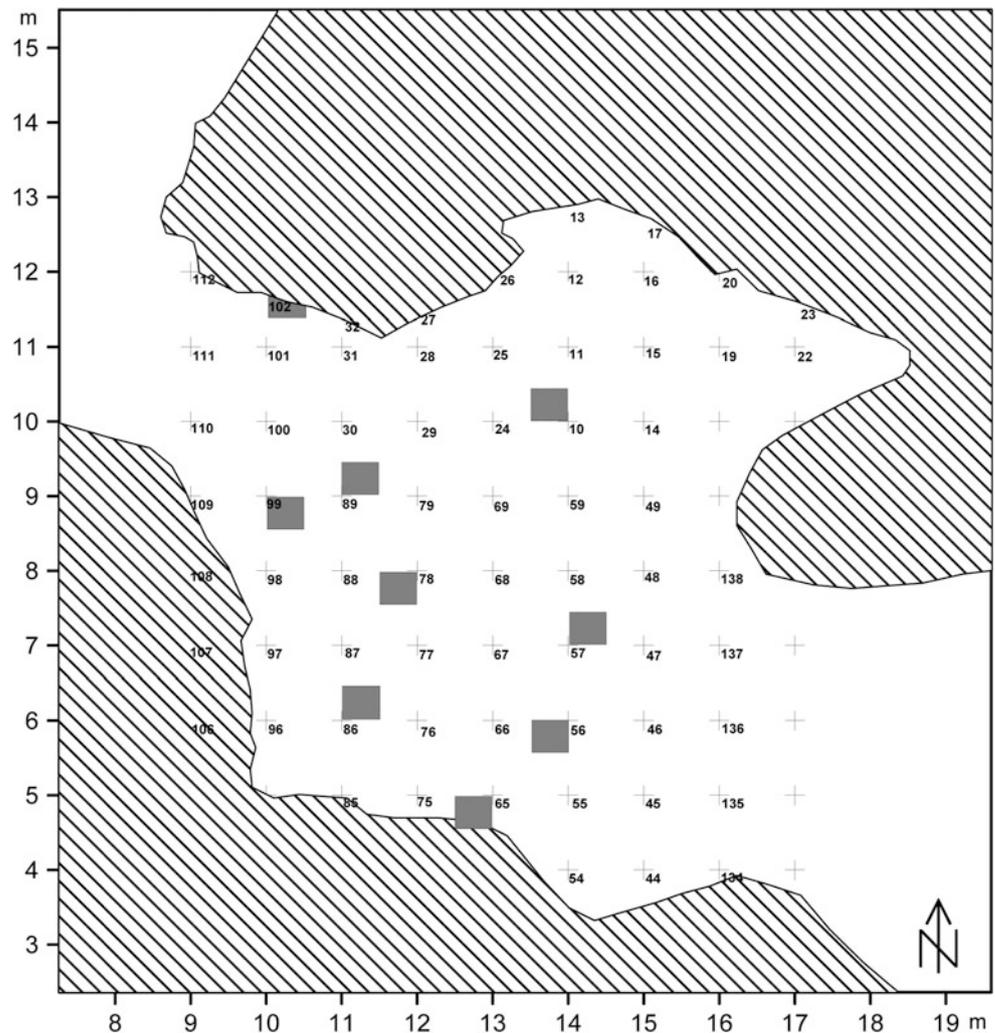
These water-screened samples are relatively unimportant for documenting the contribution of large and medium sized game to diets of Neanderthals and modern humans, because the bones of these species are larger and are usually recovered along with the ca. 22,000 and over 60,000 piece-plotted finds from Geißenklösterle and Hohle Fels.

This pilot study makes no attempt to undertake a complete analysis of all of the bones of small mammals, birds and fish recovered during water-screening. Instead, we define samples of the sediments from Geißenklösterle and from Hohle Fels. For the periods of the Upper Paleolithic,

the percentage of water-screened samples that have been analyzed is provided in the tables for birds and fish. The sample from Geißenklösterle represents the full column of sediment available from four square meters, while the sample from Hohle Fels represents the full columns available from nine quarter meters (Figs. 11.5, 11.6). Two of the nine columns from Hohle Fels span the entire stratigraphic sequence from the Middle Paleolithic to the Magdalenian, while three of the four columns sampled at Geißenklösterle extend through the Paleolithic sequence from the Middle Paleolithic to the Magdalenian. At Geißenklösterle, the central part of the excavation has mostly been dug to the bedrock. At Hohle Fels, only the central part of the excavation has reached the Middle Paleolithic find horizons, and nowhere has the bedrock yet been reached.

This situation with relatively few sampled columns extending into the Middle Paleolithic leads to a smaller amount of material from this period, and particularly affected the study of fish remains. This bias is exacerbated by the low find density of the Middle Paleolithic materials from Geißenklösterle and Hohle Fels, representing only roughly one-tenth that of the Upper Paleolithic find

Fig. 11.6 Hohle Fels. Map of the excavation showing the location of the nine quarter meters sampled for small faunal remains. Figure by M. Malina



horizons (Conard et al. 2006; Conard 2011). This means that for the Middle Paleolithic, we need a sample of roughly ten times the volume of the Upper Paleolithic strata to have a comparable sample. To help alleviate this problem, we have collected the fish remains from all the available samples from the Middle Paleolithic of Hohle Fels. We greatly increased the sample used for recovering fish bones, because our initial sample produced no remains of fish at all. At this stage of work, we are looking for the first indications of diachronic trends, and assume that more work will be needed to assess sample bias. The percentage of sampled buckets for each period is indicated in the table that presents the fish data (Table 11.7). While we acknowledge that a range of potential sampling biases as well as variable taphonomic processes and site uses exists, the available samples should give us a first reliable look at how small mammals, birds and fish contributed to hominin diet during the Middle and Upper Paleolithic.

Results

Small Mammals

At Geißenklösterle and Hohle Fels, the bones of red fox (*Vulpes vulpes*), arctic fox (*Alopex lagopus*), and especially hare (*Lepus europaeus* or *L. timidus*) occasionally preserve cutmarks documenting that a portion of the bones from these small species at these sites are the result of hominin predation (Table 11.3; Fig. 11.7). Both foxes are present in all of the periods under consideration. We grouped red fox and arctic fox as well as two hare species together since they are difficult to distinguish for fragmented specimens. Small mammals including hare and foxes form a lower portion of the faunal assemblages of Middle Paleolithic strata at Geißenklösterle than in the overlying Aurignacian and Gravettian deposits. This trend is difficult to confirm at

Table 11.3 Geißenklösterle and Hohle Fels

Taxa/body size	Geißenklösterle			Hohle Fels			
	Middle Paleolithic	Aurignacian	Gravettian	Middle Paleolithic	Aurignacian	Gravettian/Aurignacian	Gravettian
<i>Lepus sp.</i>	8	209	240	1	52	25	474
<i>V. vulpes and A. lagopus</i>	26	159	109	4	34	14	73
Indet., hare/fox size	5	75	113	10	28	13	197
Total	39	443	462	15	114	52	744

NISP of small mammals by taxa and body size

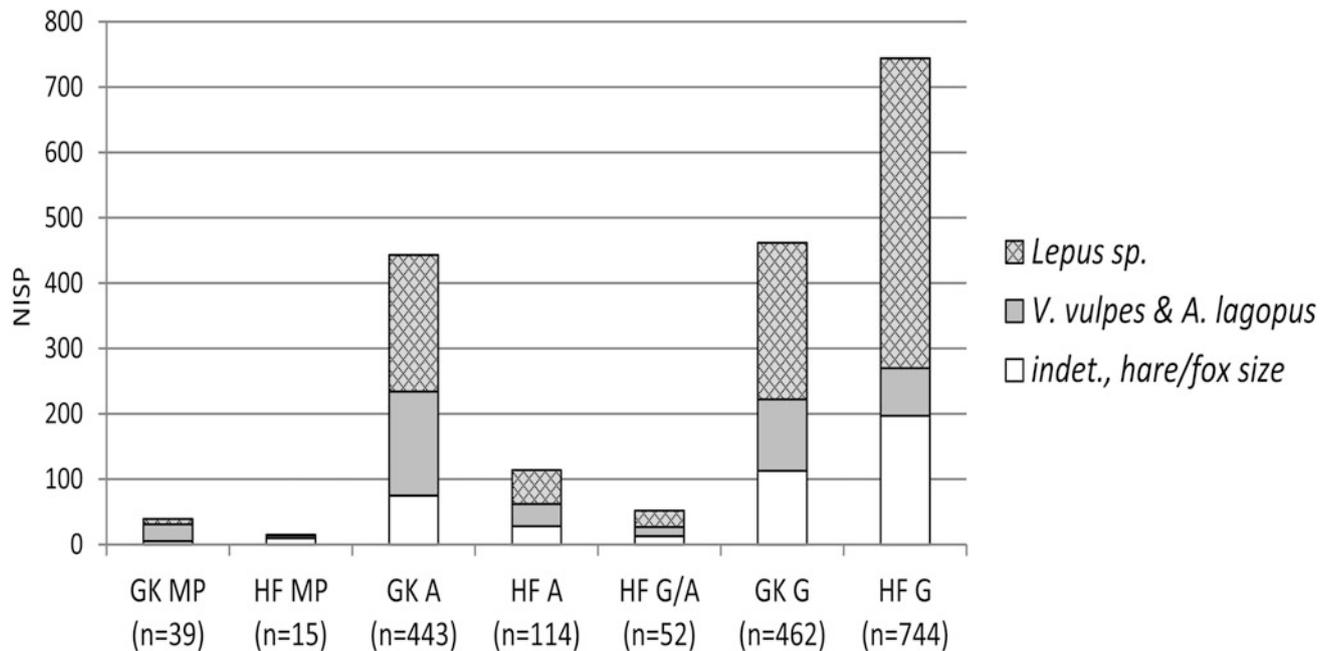


Fig. 11.7 Geißenklösterle and Hohle Fels. NISP of small mammals by taxa and body size. (GK Geißenklösterle, HF Hohle Fels, MP Middle Paleolithic, A Aurignacian, G/A Gravettian/Aurignacian, G Gravettian)

Hohle Fels because of the small size of the available Middle Paleolithic assemblage. At Geißenklösterle, where the sample size is larger, this trend is clear both in terms of NISP and bone weight.

Since the weight of edible animal resources correlates with bone weight, this parameter is the easiest means of approximating the relative contributions of species to the human diet (Uerpmann 1972, 1973). Many scholars quantify faunal remains using additional methods, such as MNI and MAU (Binford 1978), but since Brain's (1967, 1969) work demonstrated that these methods of quantification do not overcome taphonomic biases, which can depend upon biological factors such as the age at death and other post-depositional processes, we use bone weight in addition to NISP for quantifying the bones. Other attempts to quantify bone fragments cannot fully overcome issues of taphonomy (Münzel 1988; Lyman 1994; Marean et al. 2001).

Furthermore, Grayson (1984) and Lyman (1994) have shown that quantifying MNI depends on a number of assumptions, particularly on the use of carcasses by past hunters and gatherers and depends upon how assemblages are aggregated based on stratigraphic units. The parameters of NISP and bone weight can be used to approximate biomass exploited by foragers in the past. In the case of Paleolithic sites, however, the importance of faunal raw material should not be underestimated. At Geißenklösterle, we recognize a close relationship between specific skeletal elements represented in the assemblage and their use as raw materials to make tools, demonstrating that the assemblage underwent a strong selection by the site's inhabitants (Münzel 2001; Barth 2007; Barth et al. 2009).

Looking at these variables, NISP and bone weight, we see that small-sized game comprise a greater proportion of the assemblages of the Upper Paleolithic fauna than the

Table 11.4 Geißenklösterle and Hohle Fels

Taxa	Geißenklösterle			Hohle Fels			
	Middle Paleolithic	Aurignacian	Gravettian	Middle Paleolithic	Aurignacian	Gravettian/Aurignacian	Gravettian
Waterfowls	0	18	48	0	6	2	1
Birds of prey and owls	0	5	18	0	7	3	3
Galliforms	2	61	121	2	111	15	27
Songbirds	0	36	26	7	117	9	31
Others	0	16	7	0	5	0	4
Birds, ind.	0	12	28	1	74	12	39
Total	2	148	248	10	320	41	105
% of samples analyzed	Na	Na	Na	5.7	7.1	5.7	4.3

NISP of avian fauna by taxa. *Na* not available. For Hohle Fels, the sample is derived from 38 buckets from Middle Paleolithic, 143 from the Aurignacian, 78 from the Gravettian/Aurignacian, and 112 from the Gravettian

Middle Paleolithic. Since most of the cave bears in these deposits represent natural deaths and most of the mammoth ivory is associated with the manufacture of tools, ornaments and artworks, the distribution of the game species is easier to address when cave bear bones and mammoth ivory are removed from the figures (Figs. 11.2, 11.3). The Middle Paleolithic of Geißenklösterle and Hohle Fels contains 13.2 and 12.5 % small game by NISP and 0.7 and 1.6 % by weight respectively, while the Aurignacian contains 16.8 and 14.4 % by NISP and 3.1 and 4.1 % by weight respectively. The greatest change in the abundance of hare and foxes is in the Gravettian, where values go up to 39 % by NISP and 3.9–6.4 % by weight. Both Geißenklösterle and Hohle Fels show a remarkably similar signature for all periods that have sufficiently large samples (Fig. 11.7).

If we consider the pattern of faunal exploitation, we see a trend toward a greater use of hare during the Gravettian than the earlier periods. Overall, the data show that modern humans of the Upper Paleolithic exploited small mammals at higher levels than did Middle Paleolithic Neanderthals, and the increase between the Middle Paleolithic and the Aurignacian is more remarkable than the increase between the Aurignacian and the Gravettian. From this point of view, one could view this shift as a clear trend rather than a fundamental difference. Given the presence of cut marks on phalanges and metapodia, we assume that hare and foxes were often trapped for their pelts, but they were probably eaten with regularity as well. The multiple uses of small game are also demonstrated by the frequent presence of perforated fox canines as ornaments in both the Aurignacian and Gravettian of the Swabian Jura (Conard 2003). Tooth pendants are much more frequent in the Gravettian and ivory pendants are predominant in the Aurignacian.

At this stage of study, we are unsure whether hare and foxes were procured via trapping, netting, hunting or driving, and whether they carry a signal about seasonality. Similarly, it is difficult to say whether lone individuals or cooperative groups were at work. In the Gravettian and Magdalenian, the great abundance of hare is suggestive of systematically conducted group activities (Napierala 2008, 2009), while the relatively small number of faunal remains during the Middle Paleolithic and Aurignacian more likely reflect trapping or hunting of single animals.

Birds

Although most zooarchaeological work in the Swabian Jura has focused on mammalian taxa, Krönneck (2009, *in press*) and others (Götz 1949; Boessneck and von den Driesch 1973; Mourer-Chauviré 1983; Böttcher et al. 2000; Rathgeber 2004) have compiled and published data on the importance of avian fauna for Paleolithic subsistence. In the context of this study, Krönneck examined additional samples from Geißenklösterle and Hohle Fels to augment earlier data from Brillenhöhle and elsewhere. These studies indicate that game birds including galliforms, as well as other birds were hunted or trapped during both the Middle and Upper Paleolithic.

We draw our inferences on the role of birds in Paleolithic diet mainly from the study of avian faunal remains as well as from the abundance of gastroliths, because gizzard stones are abundant in fowl, especially galliforms. The fact that both of these lines of evidence point toward the same conclusions attests to the validity of the temporal trends we address here. The use of birds is also documented by feather

Table 11.5 Geißenklösterle and Hohle Fels

Taxa	Geißenklösterle			Hohle Fels			
	Middle Paleolithic	Aurignacian	Gravettian	Middle Paleolithic	Aurignacian	Gravettian/Aurignacian	Gravettian
Grey partridge, <i>Perdix perdix</i>	0	0	2	0	16	2	4
Partridge, <i>Perdix/Alectoris</i>	0	0	0	0	0	0	1
Partridge, <i>Perdicinae</i>	0	1	1	0	2	0	1
Quail, <i>Coturnix coturnix</i>	0	0	0	0	1	1	0
Hazel Grouse, <i>Tetrastes bonasia</i>	0	0	5	0	3	1	1
Ptarmigan, <i>Lagopus</i> sp.	2	49	87	0	19	2	5
Black grouse, <i>Lyrurus tetrix</i>	0	2	6	0	0	0	0
Capercaillie, <i>Tetrao urogallus</i>	0	1	2	0	0	0	0
Galliform, <i>Phasianidae</i>	0	8	18	2	70	9	15
Total	2	61	121	2	111	15	27

NISP of galliforms by taxa

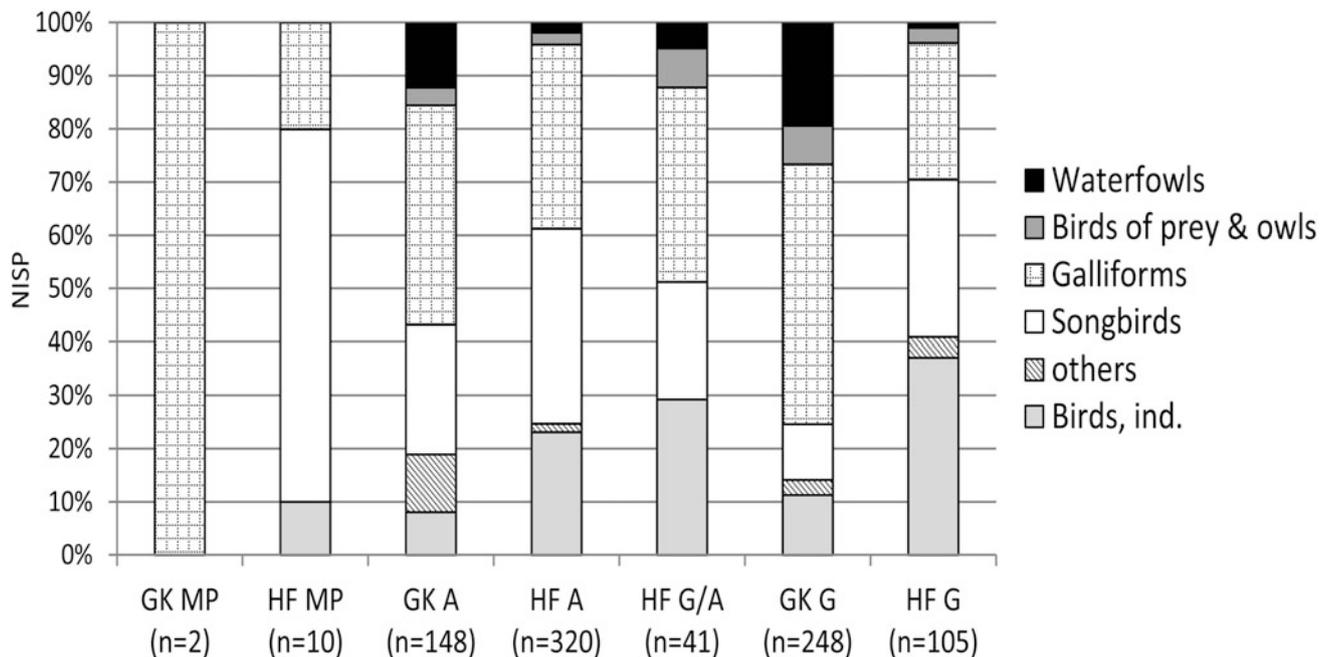


Fig. 11.8 Geißenklösterle and Hohle Fels. NISP% of avian fauna by taxa. (GK Geißenklösterle, HF Hohle Fels, MP Middle Paleolithic, A Aurignacian, G/A Gravettian/Aurignacian, G Gravettian)

fragments on stone tools in the Aurignacian context at Hohle Fels (Hardy et al. 2008).

Hohle Fels is a deep cave unsuited for owls or other roosting birds whose pellets in other settings could contribute to the avian fauna. At Geißenklösterle, the situation is less clear, but the surface preservation of the bones and

occasional anthropogenic modifications also suggest that a portion of the avian fauna is the result of activities related to human subsistence and the procurement of resources including bones for flutes and feathers.

Remains of bone flutes have been recovered from Aurignacian contexts at Vogelherd in the Lone Valley and at

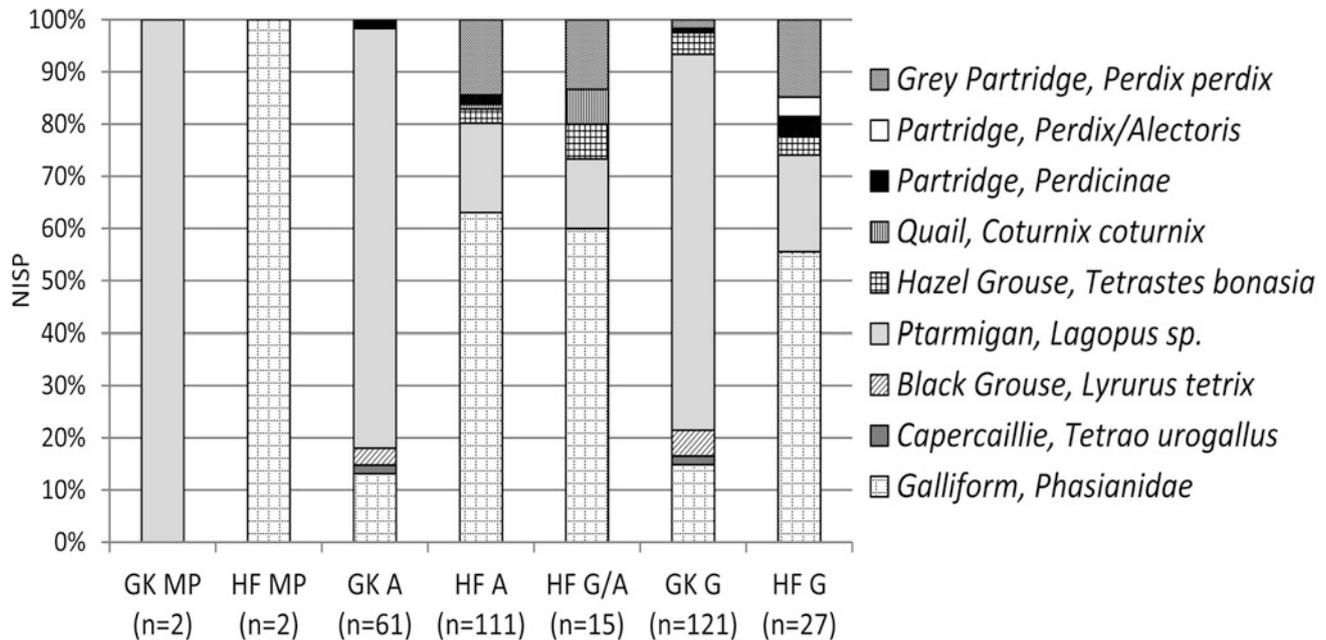


Fig. 11.9 Geißenklösterle and Hohle Fels. NISP% of galliforms by taxa. (GK Geißenklösterle, HF Hohle Fels, MP Middle Paleolithic, A Aurignacian, G/A Gravettian/Aurignacian, G Gravettian)

Geißenklösterle and Hohle Fels in the Ach Valley (Hahn and Münzel 1995; Conard and Malina 2006; Conard et al. 2009a). At Geißenklösterle and Vogelherd, the bird bone flutes appear to have been made from swan (*Cygnus* sp.) radii, and at Hohle Fels one well-preserved bone flute was carved from the radius of a griffon vulture (*Gyps fulvus*). Especially in the case of the swans, active predation is a plausible means of obtaining bones for raw material and edible resources.

The most important game bird was probably the ptarmigan (*Lagopus mutus/L. lagopus*). The ptarmigan is well represented in the Upper Paleolithic deposits of Geißenklösterle and Hohle Fels where a good sample of ptarmigan bones is available, allowing us to draw some quantitative conclusions (Tables 11.4, 11.5; Figs. 11.8, 11.9). Both sites include numerous ptarmigan bones in the Aurignacian and Gravettian. This pattern is in contrast to the Middle Paleolithic period where only few bird bones have been recovered, including two ptarmigan specimens from Geißenklösterle and two galliforms, which are slightly larger than ptarmigan, from Hohle Fels. At Hohle Fels, where gastroliths were systematically recovered, we can see that the abundance of ptarmigan bones and gastroliths co-vary with the highest values in the Aurignacian (Table 11.6; Fig. 11.10). Our data show that gastroliths are most numerous in the site's Aurignacian deposits, with the fewest present in the Middle Paleolithic deposits. The close correlation between the abundance of lithic and faunal artifacts with the presence of gastroliths also indicates that gizzard stones arrived at the sites as a result of human activities. If the gastroliths occurred in these deposits

Table 11.6 Hohle Fels

Number of specimens	Gastroliths	Galliforms
Gravettian	21	27
Gravettian/Aurignacian	14	15
Aurignacian	65	111
Middle Paleolithic	2	2
Total	102	155

Frequencies of gastroliths and galliforms

naturally, we would expect them to be equally present in archaeological find horizons and in strata lacking and poor in anthropogenic materials, which is not the case.

The remains of songbirds, particularly the jackdaw (*Coloeus monedula*), are also suggestive of human activity. One could speculate that the presence of these bones in large numbers results from collecting the young birds from their nests. This practice is well documented ethnographically (Hölzinger 1987; Fisher 1997), and possibly has contributed to the accumulation of jackdaw and other species of small songbirds. For comparison, a 250 g jackdaw is much smaller and less meaty than a 400–500 g ptarmigan or a 2000–3000 g capercaillie (*Tetrao urogallus*), or large swans that weigh 7,000–12,000 g. Taking young birds out of their nests is more like harvesting or gathering than hunting, possibly making this practice productive despite their small size.

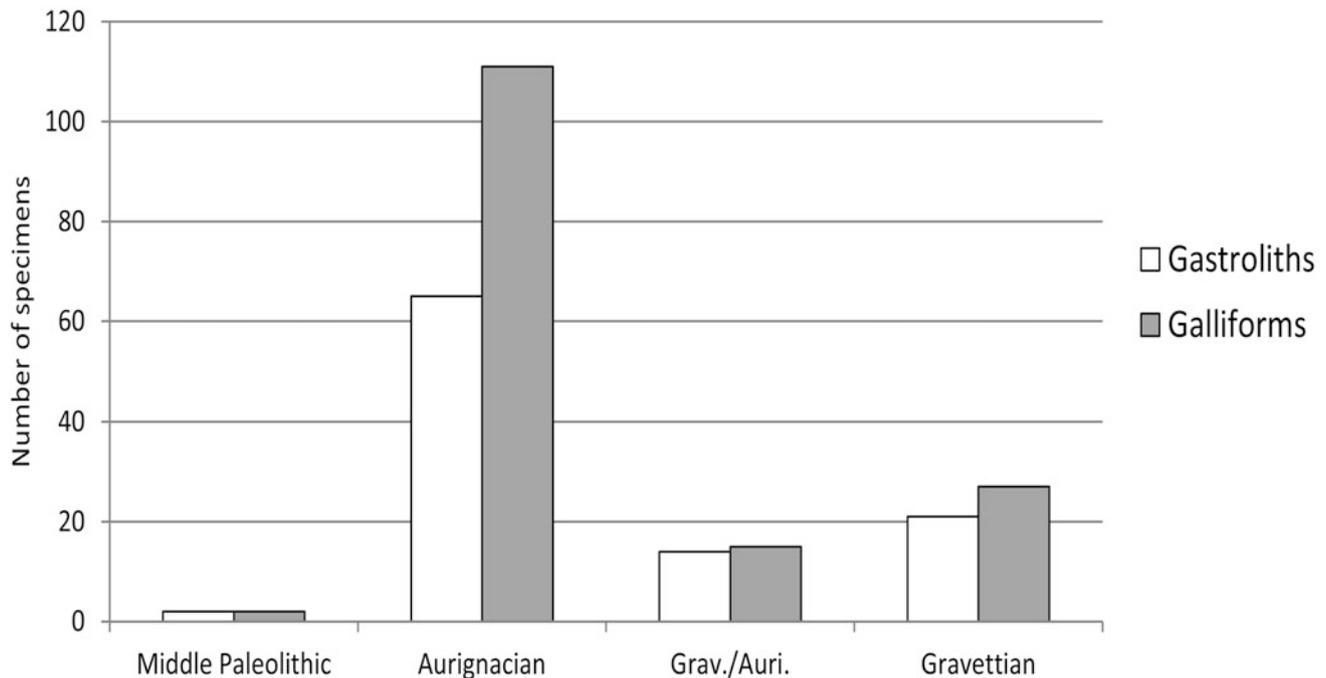


Fig. 11.10 Hohle Fels. Frequencies of gastroliths and galliforms

Bird remains are sometimes found in Middle Paleolithic sites, but are more frequent in the Upper Paleolithic (Mourer-Chauviré 1974; Laroulandie 2004; Krönneck 2009). The method used to obtain the birds is seldom clear and how the birds were used is uncertain. Birds have been documented from the Middle Paleolithic in Italy, in Fumane Cave (Peresani et al. 2011), and in France, Grotte de l'Hortus, Hérault (Laroulandie 2004). The Upper Paleolithic provides more evidence of cutmarks, use of feathers, and the production of tools and flutes. Such traces are especially common in Magdalenian contexts (Laroulandie 2004; Krönneck 2009).

In summary, the avian fauna is suggestive of a shift toward more intensive use of ptarmigan and other species beginning with the Aurignacian. This pattern of exploitation is consistent with an expansion of diet breadth in connection with increasing population densities starting at the beginning of the Upper Paleolithic.

Fish

The assemblages of fish bone provide less clear-cut evidence for a shift to new resources in connection with the colonization of southwestern Germany by modern humans and the local extinction of Neanderthals. Work on the fish from Geißenklösterle by Torke (1981) and G. Böhme and from Hohle Fels by M. Böhme has led to the identification of five

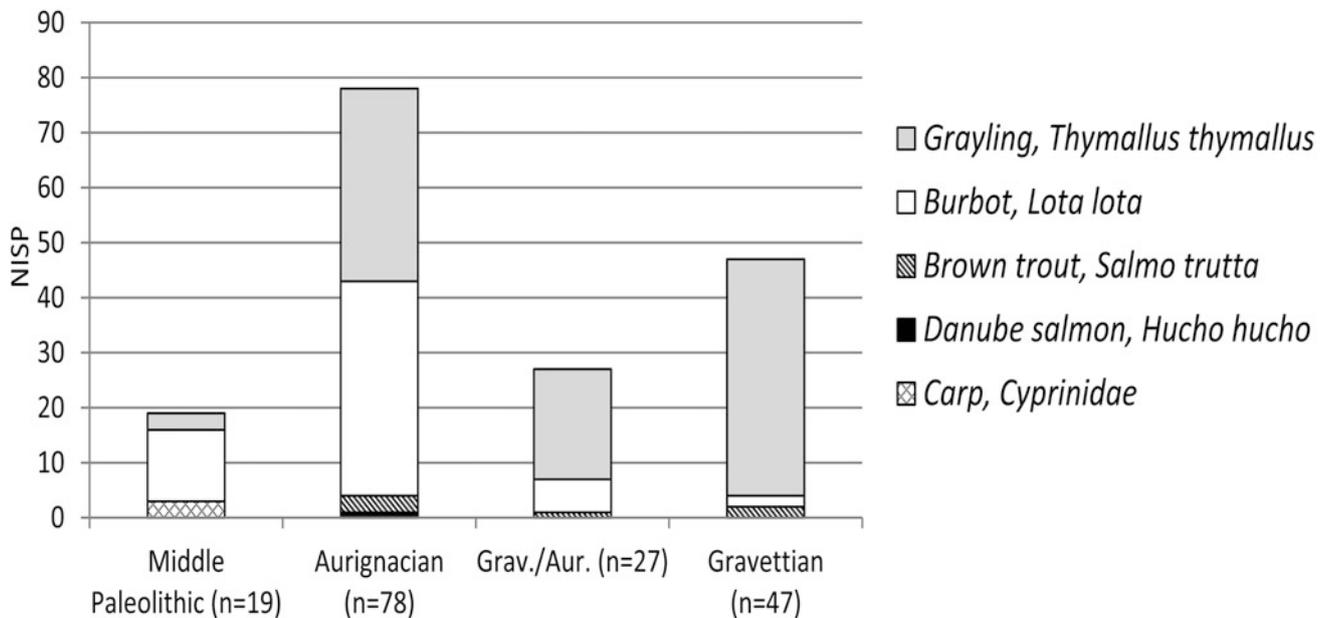
species of fish from the Danube and its tributaries such as the Ach from the Middle Paleolithic to the Gravettian (Table 11.7; Fig. 11.11). These include: carp (*Cyprinidae*), Danube salmon (*Hucho hucho*) ca. 10–15 kg, brown trout (*Salmo trutta*) ca. 500 g, grayling (*Thymallus thymallus*) ca. 500 g and burbot (*Lota lota*) ca. 500 g. Of these, all but the last have been identified by M. Böhme at Hohle Fels. The overall pattern from both sites shows similarities with common occurrences of grayling, burbot and brown trout, but a detailed comparison must await the publication of the fish remains from Geißenklösterle (Böhme *in press*).

During fieldwork at Hohle Fels, excavators occasionally identified fish bones and fish scales in the Aurignacian and Gravettian deposits. This, however, was not the case in the Middle Paleolithic deposits, where finds from all classes of anthropogenic material are less frequent. Studies of the archaeological assemblages from the caves of the Swabian Jura have demonstrated the occupation intensity during the Middle Paleolithic represents approximately one-tenth that of the Aurignacian (Conard 2011; Conard et al. 2012). To increase the likelihood of identifying the use of fish during the Middle Paleolithic, we collected the fish remains from the entire volume of the Middle Paleolithic and not just the sample columns. In this manner, we increased our sample by more than a factor of 10, making the sample roughly comparable to those from the Aurignacian and Gravettian. The abundance of the different taxa at Hohle Fels varies greatly with the common occurrence of grayling and burbot in the Aurignacian. Grayling dominates the Gravettian assemblage

Table 11.7 Hohle Fels

Taxa	Middle Paleolithic (n = 19)	Aurignacian (n = 78)	Gravettian /Aurignacian (n = 27)	Gravettian (n = 47)
Grayling, <i>Thymallus thymallus</i>	3	35	20	43
Burbot, <i>Lota lota</i>	13	39	6	2
Brown trout, <i>Salmo trutta</i>	0	3	1	2
Danube salmon, <i>Hucho hucho</i>	0	1	0	0
Carp, <i>Cyprinidae</i>	3	0	0	0
Total	19	78	27	47
% of samples analyzed	100	7.1	5.7	4.3

NISP of fish by taxa. The sample is derived from 672 buckets from Middle Paleolithic, 143 from the Aurignacian, 78 from the Gravettian/Aurignacian, and 112 from the Gravettian

**Fig. 11.11** Hohle Fels. NISP of fish by taxa**Fig. 11.12** Vogelherd. Aurignacian-aged depiction of a fish carved from mammoth ivory. Dimensions: 70.3 × 30.8 × 9.2 mm; Photo J. Lipták, copyright University of Tübingen

(Table 11.7; Fig. 11.11). The Middle Paleolithic contains only few fish remains with the majority being burbot and a few specimens of grayling and carp. The Danube salmon, which was fished in late spring (Torke 1981), is documented by only a single specimen in the Aurignacian. In addition to the taphonomic argument discussed above, the relatively large size of the species of fish present attests to the exploitation of freshwater resources by humans and not by other predators such as birds.

The overall abundance of fish rises sharply with the start of the Aurignacian, but the intensity of exploitation of fish appears to drop during the Gravettian. The Gravettian assemblage also contains a smaller number of species. In this context, one of the recently discovered ivory figurines from Vogelherd, which depicts a fish that resembles a trout, is noteworthy and provides an indication of the importance of fish for early modern humans (Conard et al. 2009b)

(Fig. 11.12). The rise in the abundance of several species of fish and the increased number of species in the diet of modern humans at the start of the Upper Paleolithic represents a change in comparison with the Middle Paleolithic, but, as with the use of small game, this change seems to reflect a more intense exploitation of fish, but not a fundamental behavioral shift.

Conclusions

The results presented here on small mammals, birds and fish complement our understanding of large mammalian game species in the past. As we have argued earlier (Münzel and Conard 2004a; Conard 2011), the use of larger mammalian species reflects continuity between the subsistence practices of Neanderthals and modern humans. In all Paleolithic periods, large- and medium-sized mammalian game, particularly horse and reindeer provided the bulk of the calories. We can now document that the start of the Upper Paleolithic during the Swabian Aurignacian saw an increased exploitation of small game. These results augment a growing body of data that documents the variability of faunal exploitation during both the Middle and the Upper Paleolithic and the diversity of the dietary shifts between the Middle and Upper Paleolithic in different regions of western Eurasia (Stiner et al. 1999; Stringer et al. 2008; Peresani et al. 2011; Blasco and Fernández Peris 2012).

We see this dietary shift in Swabia as reflecting new adaptations that allowed modern humans to maintain higher population densities. This being said, the change in diet and the use of resources is gradual when we consider the small mammalian data and the samples of fish from Hohle Fels. We see a clear intensification from both sites, but not a radical shift in prey selection. The break is seen in the leap in the exploitation at the start of the Aurignacian, but in the case of small mammals, a second and perhaps more significant shift occurs during the Gravettian. The changes reflect a mixture of continuous use of the main game species, a moderate shift in the use of small mammals and fish, and a sharp increase in the exploitation of birds during the Aurignacian.

Despite our expectations to the contrary, we have no evidence that modern humans and Neanderthals met in the Swabian Jura, and most of the sites in the region document an occupational hiatus between the late Middle Paleolithic and the Aurignacian (Schmidt 1912; Riek 1934; Hahn 1988; Conard and Malina 2003; Conard et al. 2006; Miller 2009). Still, modern humans appear to have quickly developed new practices of subsistence in the Swabian Jura that required the investment of additional effort to outcompete the indigenous Neanderthals by extracting more calories from

their environment. This increased investment in food procurement strategies allowed modern humans to feed larger groups of people and to maintain a higher population density relative to the culturally more conservative Neanderthals (Conard 2011). At this time, we also see numerous innovative lithic and organic tools and weapons that have no counterparts in the material culture of the Middle Paleolithic. Furthermore, a vast array of innovations in the symbolic realm, including figurative depictions, mythical imagery, personal ornaments with three dimensional forms and musical instruments also emerge (Conard 2008, 2009; Conard et al. 2009a). While these important innovations cannot be explained solely in terms of dietary and nutritional variables, the evidence for expanding diet breadth and intensified extraction of animal resources from the environment likely contributed to the demographic success of modern humans and the ultimate extinction of Neanderthals.

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